Is It a Deme, a Stock, or a Subspecies?
These and Other Definitions

By

Robert L. Wilbur

Jim Seeb

Lisa Seeb

and

Hal Geiger

Regional Information Report[1] No. 5J98-09

Alaska Department of Fish and Game
Commercial Fisheries Management and Development Division
Juneau, Alaska

March 1998

[1] The Regional Information Report Series was established in 1987 to provide an information access system for all unpublished divisional reports. These reports frequently serve diverse ad hoc informational purposes or archive basic uninterpreted data. To accommodate timely reporting of recently collected information, reports in this series undergo only limited internal review and may contain preliminary data; this information may be subsequently finalized and published in the formal literature. Consequently, these reports should not be cited without prior approval of the author or the Division of Commercial Fisheries.

INTRODUCTION

These population-based definitions were originally prepared in 1996 to aid the Alaska Board of Fisheries in developing consistent applications for the terms used in their guiding principles, and to assist in dialog related to improving management of fish populations. They are archived in this report for reference purposes with only minor changes from the draft originally reviewed by the board 2 years ago. These terms are important because application of the board's guiding principles can affect the management regimes the board selects to achieve its objectives. These decisions will significantly influence the future long-term well-being of fish stocks, as well as the socioeconomic well-being of the resource users. Therefore, it is important the terms be clearly understood for not only their literal meaning, but more importantly, for their pragmatic use in the real world of Alaska's fisheries management.

However, while an improved understanding of genetics and conservation biology may promote practical management applications, the sum total of all factors controlling populations is extremely complex and includes anthropogenic factors, such as fishing, habitat loss, pollution, and global warming. Because our contemporary knowledge of some of those factors is very limited and because those factors can overwhelm management influences, developing effective management strategies can be difficult to research and authenticate.

The following definitions appear in alphabetical order and include sections on related words and related bibliographic materials. Related words in italics are defined among the listed definitions while unitalicized words are not included. The bibliographic reading section includes citations to relevant literature listed in the bibliography, but not all references in the bibliography are included under the definitions.

This list is not complete or all-inclusive; it is a first attempt at compiling the many definitions and associated scientific debates of the terms used in the guiding principles.

DEFINITIONS

Adaptive Management

Definitions: The term *adaptive management* is not well defined, but it generally refers to a style of natural resource management characterized by deliberate experimental policies to determine the limits of the resource and a strategy that adaptively changes based on the information gained. The notion of altering a management strategy, in a highly organized way in response to feedback, is common to the way most people use the term. For example, Ministry of Forests for the Province of British Columbia[1] states, "Adaptive management rigorously combines management, research, monitoring, and means of changing practices so that credible information is gained and management activities are modified by experience." Adaptive management is based on the premise that natural resources are generated by complex and unpredictable systems, that certain understanding of the principles that drive the system is impossible. It

[1] Taken from the Province of British Columbia Ministry of Forests Internet page on Adaptive management, http://www.for.gov.bc.ca/pab/publctns/glossary/glossary.htm, on Thursday, October 17, 1996.

follows that the management strategy should constantly change and adapt to take advantage of what has been learned to date, and that management should take actions that will lead to new understanding of the system in the future.

Walters (1986) refers to a range of adaptive policies, from *actively adaptive*, where learning about the resource becomes one of the yields of the resource, at the expense of other forms of yield, to *passively adaptive*, where the policy is just to collect information and attempt to use whatever knowledge is gained to alter the management course.

The basic underpinnings of adaptive management come from the field of process control engineering, and much of the adaptive management literature is quite mathematical in nature. Hilborn and Walters (1992) describe adaptive management as a combination of two approaches:

> A management authority. . .[1] may make an initial choice that 'looks reasonable' on intuitive grounds, then plan to systematically vary the choice while monitoring biological and economic responses, so as to eventually find the best choice by an empirical process of trial and error. . . [2] it may engage in formal stock assessment, the construction of quantitative models to make the best predictions possible about alternative choices based on whatever data are available to date, and then base its choices on the models while expercting to refine or modify the choices later as more data become available.

In fisheries, formal Bayesian probability theory is often used to quantify how the understanding of the state of the resource changes, and the resource is often described in terms of yield, stock-recruit relationships, and surplus production models.

Related Words: stock-recruit relationship, surplus production models

Bibliographic Reading: Hilborn et al. 1980; Holling 1973, 1978, 1989; Lee 1993; Lee and Lawrence 1986; Ludwig and Walters 1981; Ludwig et al. 1993; Smith and Walters 1981; Walters 1986; Walters and Hilborn 1976; and Walters and Holling 1984.

Biological Diversity

Definition: *Biological diversity* or *biodiversity* is defined as "all hereditarily based variation at all levels of organization, from the gene within a single local population or species, to the species composing all or part of the local community, and finally to the communities themselves that compose the living parts of the multifarious ecosystems of the world" (Reaka-Kudla et al. 1997). The study of biodiversity includes not only the study of living organisms at all levels, from genetics through species to higher taxonomic levels, but also the interaction with habitats and ecosystems (Meffe and Carroll 1994).

Related Words: *effective population size, evolutionarily significant unit, genetic diversity*

Bibliographic Reading: Allendorf and Leary 1988; Allendorf and Waples 1996; Baskin 1994; and Reaka-Kudla et al. 1997.

Deme *(see local population)*

Effective Population Size (N_e)

Definitions: Effective population size (N_e) is a useful concept for estimating the expected rate of loss of genetic variation in isolated populations, and it is often considerably less than absolute or census number of individuals (N_c). N_e is a measure of the population of breeding individuals produced each generation by random union of an equal number of male and female gametes randomly drawn from the previous generation (Wright 1969). In other words, it is a population in which every individual has an equal probability of contributing genes to the next generation with the assumptions that the population is randomly mating with discrete generations, equal sex ratios, even progeny distribution, and no selection (Crow and Kimura 1970). To the extent that these assumptions are violated, N_e will be less than N_c (Nelson and Soulé 1987).

There are few trustworthy estimates of N_e in natural population (Ryman et al. 1981). In natural populations, N_e is extremely hard to measure, and it may be very much smaller than the census population (Simon et al. 1986; Nelson and Soulé 1987). Various authors have suggested ratios of N_e / N (Soulé 1980; Nelson and Soulé 1987), and these ratios vary from 50% to 10% for fish populations.

However, Pacific salmon with the exception of pink salmon do not have discrete generations, an important assumption in the calculation of N_e. Statistical estimation of N_e for salmonids has been given by Tajima (1992). Waples (1990) using simulations suggested that multiplying effective number of breeders in any given year (N_b) by the average age of reproduction gives a suitable estimate of N_e. Specifically, $N_e = gN_b$ where g is the generation length or average age of spawning.

Related Words: *extinction*, founding population, *minimum viable population*

Bibliographic Reading: Begon 1977; Gilpin and Soulé 1986; Lande and Barrowclough 1987; Ryman et al. 1981; and Tajima 1992.

Endangered Species

Definitions: The Endangers Species Act defines an *endangered species* as "any species which is in danger of extinction throughout all or a significant portion of its range other than a species of the Class Insecta determined by the Secretary (Departments of Interior, Commerce, or Agriculture as appropriate) to constitute a pest whose protection under the provisions of this Act would present an overwhelming an overriding risk to man."

Related Words: *species, subspecies*, population segment, *threatened species*

Bibliographic Reading: Angermeier and Williams 1994; Hyman et al. 1993; Nehlsen et al. 1991; NRC 1995; Public Law 100-478, October 7, 1988, Endangered Species Act of 1973 as amended through 1988; and Utter 1980.

Evolutionarily Significant Unit (ESU)

Definitions: *Evolutionarily significant units (ESUs)* were as originally suggested in 1985 by the American Association of Zoological Parks and Aquariums as an alternative to *subspecies,* their frustration with *subspecies* being that the term was arbitrary and meaningless (Ryder 1986), as anecdotally epitomized by cases in which two separate subspecies were named from littermates. Following their describing and coining of ESU, Waples (1991c) gave the term prominence by proposing its use in defining populations for the purpose of possible protection under the Endangered Species Act (ESA). Waples defined an ESU as follows:

> A vertebrate population will be considered distinct (and hence a "species") for purposes of conservation under the Act if the population represents an evolutionarily significant unit (ESU) of the biological species. An ESU is a population (or group of populations) that:
>
> (1) Is substantially reproductively isolated from other conspecific population units, and
> (2) Represents an important component in the evolutionary legacy of the species.

According to Waples the reproductive isolation "must be enough to allow evolutionarily important differences to accrue." The evolutionary legacy refers to the heritable material that an ESU must possess and be capable of "carrying forward into the future," and of course that heritable material must be important to the species by having unique characteristics not common in other ESUs.

The legislative history of the ESA indicated that the act was to protect genetic diversity without becoming excessive — that is, "to list populations sparingly and only when biological evidence indicates that such action is warranted" (Waples 1991c). The ESU concept was therefore developed to eliminate insignificant or genetically nonunique populations from being designated as "species" under the act. By adding the two ESU criteria for the "species" designation under the act, ESUs presumably reduced the number of populations that would otherwise have been candidate for consideration.

Related Words: conspecific, gene flow, reproductive isolation, *species*, *subspecies*

Bibliographic Reading: Backman and Berg 1992; Fox 1991; Hyman et al. 1993; Nielsen 1993; NMFS 1978; Rohlf 1991; Utter et al. 1993; Waples 1991a,b,c; and Waples 1995.

Extinct (Extirpate)

Definitions: Random House Unabridged Dictionary defines *extinct* as a adjective meaning "no longer in existence; that has ended or died out," and *extinction* as a noun of the same meaning. It defines extirpate as a verb meaning "to remove or destroy totally; do away with."

In biological usage *extirpate* is usually describes the elimination of a population from an area or the eradication of a species.

Related Words: exterminate, eradicate

Bibliographic Reading: CPMPNAS 1996; Dobzhansky 1950; Lande and Orzack 1988; and Richter-Dyn and Goel 1972.

Fitness

Definitions: Darwin's notion of *fitness* was based on reproducibility of the individual; i.e., a highly fit individual produced many more offspring than one that was not particularly fit, hence the survival of the fittest (Darwin 1859). That notion of fitness was then applied to populations and to species.

Fitness in population genetics is a quantitative measure of reproductive success of a given genotype, i.e. the average number of progeny left by this genotype as compared to the average number of progeny of other competing genotypes *F* (Rieger et al. 1991).

Related Words: natural selection, genotype

Bibliographic Reading: Darwin 1859; and Kapuscinski 1984.

Genetic Diversity

Definitions: *Genetic diversity* refers to all genetic variation both within and among populations and species. This variation can be partitioned and studied in a hierarchical manner. A typical hierarchy might include variability within individuals, among individuals within populations, and among populations within species. Conservation of genetic diversity requires conservation at all levels of the hierarchy (Allendorf et al. 1987).

Related Words: biodiversity, fixed allele, genetic drift, heterozygosity, migration, mutation,

Bibliographic Reading: Allendorf and Leary 1988; Allendorf and Waples 1996; Crow and Morton 1955; CPMPNAS 1996; Grant 1963; Lacy 1987; Meffe and Carroll 1994; Nei 1987; Nelson and Soulé 1987; and Waples 1990.

Local Population (Population, Deme)

Definitions: Random House Unabridged Dictionary (Flexner 1993) lists six varied definitions for the term *population*, including statistical and demographic definitions. The biological definition is "all the individuals of one species living in a given area, or the assemblage of a specific type of organism living in a given area." Given the variety of *population* definitions and because populations represent the major biological unit between individuals and species (Mayr 1963), ecologists wanted a biological term for *population* that was unencumbered by other meanings.

Local population — that is, a group of interbreeding organisms sharing a defined locale — became and remains a popular replacement for *population*. A local population composes a gene pool, which means that theoretically any individual within the local population has an equal chance of mating with any other individual of the opposite sex within the local population. Although this panmictic view of breeding in reality is not generally held to be particularly accountable in real local populations, the concept of spatial distinctiveness is central to defining local populations of a species.

The term *deme,* was first suggested by Gilmour and Gregor (1939) as a synonym for *population*, but as *population* gave way to *local population*, Wright (1955) and others suggested *deme* as the synonym for *local population*. This suggestion is well accepted today.

Related Words: population segment, *metapopulation, subspecies*

Bibliographic Reading: Allendorf 1983; Gilmour and Gregor 1939; Gilmour and Heslop-Harrison 1954; Mayr 1963; Nei 1972; Rich 1939; and Wright 1940, 1951, 1969.

Metapopulation

Definition: The term *metapopulation* refers to an aggregation of patchily distributed local populations that are interconnected by migration corridors between the local populations. While there is some degree of migration between local populations, the chances of an individual from one local population mating with that of another population is far less than the chances of its mating with an individual within its deme. Were the same individuals composing a metapopulation to instead form one large continuous population such that the chances for any individual mating with any other individual were approximately the same, then the evolutionary framework of the population could be quite different than it would be as a metapopulation. In some species metapopulations are naturally occurring, but in other species large continuous populations may have been converted to metapopulations by anthropogenic factors, such as destruction of a continuous habitat into patches of habitat.

Related Words: *Deme, local population*, overlapping populations

Bibliographic Reading: Allendorf 1983; CPMPNAS 1996; and Wright 1940, 1951, 1969.

Minimum Viable Population (MVP)

Definitions: The concept of viable population or "what is enough" has interested biologists from a wide range of disciplines and is one of the more difficult and challenging problems in conservation biology. Soulé (1987) states the question of what is a viable population more specifically: "What are the minimum conditions for the long-term persistence and adaptation of a species or population in a given place?" Often the concept of viable population has been equated with minimum viable population or MVP and has lead to extensive studies in population viability analysis (PVA) (see chapters in Soulé 1987). These studies cross disciplines and include considerations drawn from ecology, population dynamics, genetics as well as habitat and climatic considerations. However, there is a general consensus that there is not single value or "magic number" that has universal validity (Soulé 1987).

The term minimum viable population (MVP) was proposed by Schaefer (1981) as "a minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1,000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes."

The concept has evolved to refer to the smallest isolated population size that has a specified percent chance of remaining extant for a specified period of time in the face of foreseeable demographic, genetic, and environmental stochasticities, plus natural catastrophes (Meffe and Carroll 1994). The level of risk (probability of persistence) can be adjusted on a case by case basis. For example, in certain cases a 50% probability of persistence for 100 years might be acceptable, while in other cases a 99% probability of persistence for 1000 years might be recommended (Soulé 1987). The National Research Council recently reviewed the factors involved in estimating risk under the ESA (NRC 1995).

National Marine Fisheries Services undertook an extensive review of the question of minimum viable populations under the ESA with specific reference to Pacific salmon (Thompson 1991). Thompson (1991) outlined three types of approaches for determining MVP: (1) population genetic considerations or "rules of thumb", (2) analytic approaches, and (3) simulation. The "rules of thumb" were proposed by Franklin (1980) and Soulé (1980). They have been termed the "50/500" rules because they prescribe a short-term effective population size (N_e) of 50 to prevent an unacceptable rate of inbreeding and a long-term N_e of 500 to maintain overall genetic variability. It is important to recognize that effective population size can be much smaller than the census number (ADF&G 1985). Analytic approaches include population genetic models (Crow and Kimura 1970; Franklin 1980; Lande and Barrowclough 1987), birth-and-death process (MacArthur and Wilson 1967; Goodman 1987), and diffusion models (Dennis et al. 1991). Examples of simulation approaches include those of Schaefer (1981), Lande and Orzack (1988), and Dennis et al. (1991).

Related Words: *extinction,* founding population, *genetic viability*

Bibliographic Reading: Carson 1983; CPMPNAS 1996; Franklin 1980; Gilpin and Soulé 1986; Richter-Dyn and Goel 1972; Schaefer 1981, 1990; and Thomas 1990.

Species

Definitions*:* In Linnaean terms *species* were believed to arbitrary units developed for purposes of scientific convenience; species were characterized by consistency and morphological delimitation. As Darwin (1859) explained, "[the term species] does not essentially differ from the term variety which is given to less distinct and more fluctuating forms." This *typological* or *morphological* concept of a species may have reached its peak when some taxonomists even tried to decipher species based on percentages of shared and unique morphological characteristics (Ginsburg 1938). The morphological species concept began to fall apart when systematists realized that it did not work well for some species that demonstrated considerable polymorphic diversity or when two species shared extremely similar morphologies. Concurrently they began to recognize the concept treated *species* as an assemblage of inanimate objects, which for groups of naturally reproducing organisms seemed inappropriate.

The concept of species as a natural unit rather than an arbitrary one was first proposed by Ray (1686) and was furthered by Koeler in 1760 who suggested that individuals belong to a species if they produce fertile offspring. The *cross-fertility species concept* failed when it was recognized that "many fully cross-fertile animals may live side by side without interbreeding because their reproductive isolation is maintained by isolating mechanisms other than the sterility barrier" (Mayr 1963).

This gave rise to the *nondimensional species concept,* which proposed that species were groups that shared the same geographic area (sympatric) at the same time but were not the same (i.e., they were discontinuous), even though their physical differences might be barely perceptible. The concept introduced the notion of interbreeding individuals as the criterion for determining species. Its shortcoming was that it failed to recognize that individuals that are geographically separated (allopatric instead of sympatric) may belong to the same species.

Mayr's (1940) definition produced the modern concept of a species as "groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups." Dobzhansky (1950) offered a similar definition: "[a species is] is the largest and most inclusive . . . reproductive community of sexual and cross-fertilizing individuals which share a common gene pool." The *biological species concept* emphasized three aspects of a species (Mayr 1963):

(1) Species defined by distinctness rather than difference.
(2) Species consist of populations, not individuals.
(3) Species express reproductive isolation among sympatric populations.

While this concept remains conceptually defensible today, it has lost its much of its preeminence because applying it to allopatric populations (i.e., actually determining "potentially interbreeding") and some parthenogenic species (all female) is impractical and presumptuous. It is being challenged today by the *evolutionary concept* of a species (Wiley 1981), which indicates that species are "a single lineage of ancestor-descendant populations which maintains its identify from other such lineages and which has its own evolutionary tendencies and historical fate." A related species definition, the *phylogenetic concept*, is even more restrictive: as described by Utter et al. (1993) a species is "the smallest detectable population with unique sets of characters."

These species concepts evolved because new techniques to assess genetic relations (e.g., biochemical analyses) provide new and presumably more reliable measures of species designations than did the interbreeding criteria. The concepts also redefine species to the population level, which evolutionary biologists today believe is the level at which evolution occurs, rather than at the biological species level. However, systematists still adhere to the biological concept for delineating species, at least in part to maintain a functional system of nomenclature.

The Endangered Species Act (ESA) definition of *species* embraces the evolutionary/phylogenetic concepts; that is, a species includes "any subspecies of fish or wildlife or plants and any distinct population segment of any species or vertebrate fish or wildlife which interbreeds when mature." From the ESA species definition, the *evolutionarily significant unit (ESU)* was developed (Waples 1991c) as an approach to defining what was meant by "population segment" based on the historical intent of the act, which sought to protect "losses of genetic variations." In a pragmatic sense then, *ESU* becomes a synonym for *species* as defined by ESA.

Related Words: *endangered species, evolutionarily significant unit, threatened species*, polytypic species, reproductive isolating mechanisms, sibling species, speciation, *subspecies*, sympatric/allopatric

Bibliographic Reading: Darwin 1859; Ginsburg 1938; Grant 1963; Mayr 1963; Otte and Endler 1989; Ray 1686; Utter et al. 1993; Waples 1991b; and Wiley 1981.

Stock

Definitions: Random House Unabridged dictionary defines *stock*, as generally applied to wild fauna and flora, as: "a race or other related group of animals or plants" (Flexner 1993). However, the dictionary also lists 60 other widely varied definitions of *stock*, which suggests that use of the word in the biological sciences was borrowed from the common language and did not have a scientific origin. Agrarian uses of *stock* probably preceded and gave rise to biological applications.

Busack and Marshall (1995) define stock as "a group of interbreeding individuals that is genetically distinct and substantially reproductively isolated from other such groups." They appear to have developed their notion of a stock from Ricker's (1972) definition: "fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to a substantial degree do not interbreed with any group spawning in a different place." Underlined in both these definitions is the word "substantial," which introduces much more scientific subjectivity than is found in the biological definition of *species* and makes actual identification of stocks more problematic.

The basic tenet is that if introgression between two spatially or temporally distinct interbreeding groups is substantial, then the two groups may actually be one group or subcomponents of an even larger group. *Substantial* has not been objectively defined, probably because no scientist wants to open that Pandora's Box. The other part of the problem is that we rarely know how much introgression is occurring between such groups of fish. A variety of techniques that determine genetic uniqueness and similarity between such groups can be used to index levels of introgression, but they are expensive and labor intensive, and as more data are developed from different collections, the job of separating distinct stocks from the continuum of data points becomes ever more difficult and subjective.

An objective definition of a stock is suggested by Booke (1981): "a population of fish that maintains and sustains Castle-Hardy-Weinberg equilibrium." This equilibrium refers to stability of allelic proportions within a spawning population, indicating a balance in the rate at which undesirable alleles are introduced and eliminated from the population. This definition, while philosophically sound, is not particularly pragmatic because Hardy-Weinberg equilibriums are even more difficult to validate with real data.

From the fisheries management perspective of a stock was based on the need to somehow lump fish together into units that could be managed. Larkin (1972) indicated that a stock was any group of populations separately fished; similarly Ricker's (1975) management-based definition of stock was "the part of a fish population which is under consideration from the point of view of actual or potential utilization." This differed from Ricker's (1972) biological stock concept, which was based on interbreeding and genetic consistency. It ignores those considerations and defines stocks as groups that share temporal and spatial migration patterns and are therefore managed as a unit to provide some desired split between fishery catch and a target number of spawners. While some of these stocks may actually represent true biological stocks, such occurrences would be coincidental; most stocks delineated by management capability could instead include from a fraction of one to many biological stocks.

Ricker's (1975) management definition, however, fails to recognize that fishery managers frequently identify stocks based on geographic or temporal distinctiveness or separation of spawning areas, which they assume represent the natal source for most of the subsequent interbreeding adults. It is the numbers of individuals composing these groups that managers rigorously seek to estimate each season, under the notion that some specific number is needed to sustain that interbreeding group into the future. Whether the spawners occupying those areas can be discretely managed or must be managed in aggregate with other stocks is not particularly relevant. This management-based concept of *stock* is reflected by Van Alen (*in press*), and seems to be more widespread among managers than than Ricker's management definition. However, Ricker's management definition of *stock* is quite close to Van Alen's definition of a *stock group*:

> *Stock group*: a term originating with salmon management that refers to geographic groupings of two or more stocks that experience similar environmental influences and have similar migration routes and timing. This enables stock groups to be managed as discrete units; thus, stock groups share common patterns of exploitation because management actions similarly harvest or protect fish in a stock group. For all these reasons, stocks in a stock group presumably have similar levels of productivity.

Evolutionarily significant units, which arose from the Endangered Species Act as a policy for protecting evolutionarily unique genetic stocks, further confused the stock concept and led to divisiveness among managers and conservation biologists.

Ambiguity and disparity in these *stock* concepts has lead to recent discrediting of the use of *stock* in conservation biology and use of the word *deme* instead (CPMPNAS 1996; Geiger and Gharrett 1998). Geiger and Gharrett further suggest that *stock* should be limited to fisheries management uses.

Related Words: *deme, evolutionarily significant unit (ESU), local population, metapopulation*, race

Bibliographic Reading: Allendorf et al. 1987; Booke 1981; Dobzhansky 1950, 1970; Fox 1991; Geiger and Gharrett 1998; Ginsburg 1938; Helle 1981; and Larkin 1972.

Subspecies

Definitions: *Subspecies* as a taxonomic term entered the systematists' common language in the 1800s, and like the term *species* was assigned the same sort of typological definition, the only difference being that it was one taxonomic unit below species. Mayr (1963) defines *subspecies* as "an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species." That is, a subspecies is designated by measurable or visible morphological and geographical differences. Often the morphological differences are subtle and even less distinct in areas where their respective portions of the species range overlap.

Subspecific epithets are included as the third part of the binomial scientific species name. For example, Atlantic and Pacific herring were until recently believed to be two subspecies: *Clupea harengus hargenus* and *C. harengus pallasi*, respectively. Based on a study of their biochemical genetics, they were reclassified as two separate species: *C. harengus* and *C. pallasi*, respectively.

Mayr (1954) suggested abandoning use of the term *subspecies* because it is arbitrary and exists only for the convenience of pigeonholing morphologically distinct geographic isolates of a species and, as such, is a category that lacks evolutionary and biological pertinence. As Mayr (1963) described:

> Whenever a thorough biometric-morphological analysis established a mean difference between the samples, this was considered sufficient justification by these authors to describe a new subspecies. In the more intensely studied groups of animals this approach has led to a wild-goose chase for new subspecies, and has seriously impaired the usefulness of the subspecies category. . .The better the geographic variation of a species is known, the more difficult it becomes to delimit subspecies and the more obvious it becomes that many such delimitations are arbitrary.

Reduced attention to subspecies is underway largely because modern genetic techniques, by which genetic distance between populations is being determined, have produced greater interest on the evolutionarily significant population and less interest in the arbitrary clumping of populations into subspecies that sometimes, if not often, have proved weakly founded (Ryder 1986).

Related Words: *evolutionarily significant unit (ESU),* genetic distance, race, *species*, variety (plants)

Bibliographic Reading: Grant 1963; and Mayr 1963.

Threatened Species

Definitions: Under the Endangered Species Act a *threatened species* is any species that is likely to become an *endangered species* within the foreseeable future throughout all or a significant portion of its range.

Related Words: *endangered species*, population segment, *species, subspecies*

Bibliographic Reading: Angermeier and Williams 1994; Hyman et al. 1993; Nehlsen et al. 1991; NRC 1995; Public Law 100-478, October 7, 1988, Endangered Species Act of 1973 as amended through 1988; and Utter 1980.

BIBLIOGRAPHY

ADF&G (Alaska Department of Fish and Game). 1985. Genetic Policy. Alaska Department of Fish and Game, Division of Fisheries Rehabilitation, Enhancement, and Development, FRED Special Report, Juneau.

Allendorf, F. W. 1983. Isolation, gene flow, and genetic differentiation among populations. Pages 51–65 *in* C. M. Schonewald-Cox, S. Chambers, B. MacBryde, and L. Thomas, editors. Genetics and conservation. Benjamin Cummings Publishing Company, Menlo Park, California.

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170–184.

Allendorf, F. W., and N. Ryman. 1987. Genetic management of hatchery stocks. Pages 141–159 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Allendorf, F. W., N. Ryman, and F. Utter. 1987. Genetics and fishery management: past, present and future. Pages 1–19 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Allendorf, F. W., and R. S. Waples. 1996. Conservation and genetics of fishes in the Salmonidae. *In* J. C. Avise and J. L. Hamrick, editors. Conservation genetics: case histories from nature. Chapman & Hall, New York.

Angermeier, P. L., and J. E. Williams. 1994. Conservation of imperiled species and reauthorization of the Endangered Species Act of 1973. Fisheries 19:26–29.

Backman, T. W. H., and L. Berg. 1992. Managing molecules or saving salmon? The evolutionarily significant unit. Columbia River Inter-Tribal Fish Commission, Wana Chinook Tymoo 2:8–14.

Bartley, D. M., B. Bentley, J. Brodziak, R. Gomulkiewicz, M. Mangel, and G. A. E. Gall. 1992. Geographic variation in population genetic structure of chinook salmon from California and Oregon. Fisheries Bulletin 90:77–100.

Baskin, Y. 1994. Ecologists dare to ask: how much does diversity matter? Science 264:202–203.

Becker, W. A. 1984. Manual of quantitative genetics, 4th edition. Academic Enterprises, Pulman, Washington.

Begon, M. 1977. The effective population size of a natural *Drosophila subobscura* population. Heredity 38(1):13–18.

Booke, H. E. 1981. The conundrum of the stock concept — are nature and nurture definable in fisheries science? Canadian Journal of Fisheries and Aquatic Sciences 38(12):1479–1480.

Bormann, B. T., P. G. Cunningham, M. H. Brookes, V. W. Manning, and M. W. Collopy. 1994. Adaptive ecosystem management in the Pacific Northwest. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR0341, Portland.

Brown, B. 1982. Mountain in the clouds: a search for wild salmon. Simon and Schuster, New York.

Busack, C. A., and K. P. Currens. 1995. Genetic risks and hazards in hatchery operations: fundamental concepts and issues. Pages 71–80 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15, Bethesda, Maryland.

Busack, C., and A.R. Marshall. 1995. Defining units of genetic diversity in Washington salmonids. Chapter A *in* C. Busack, and J.B. Shaklee, editors. Genetic diversity units and major ancestral lineages of salmonid fishes in Washington. Washington State Department of Fish and Wildlife, Olympia.

Campton, D. E. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: what do we really know? Pages 337–353 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15, Bethesda, Maryland.

Carson, H. L. 1983. The genetics of the founder effect. Pages 189–200 *in* C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. Genetics and conservation. Benjamin Cummings Publishing Company, Menlo Park, California.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Reviews in Biology 29:103–137.

Compton, D. E., and F. M. Utter. 1987. Genetic structure of anadromous cutthroat trout (*Salmo clarki clarki*) populations in the Puget Sound area: evidence for restricted gene flow. Canadian Journal of Fisheries and Aquatic Sciences 44:573–582.

CPMPNAS (Committee on Protection and Management of Pacific Northwest Anadromous Salmonids). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, DC.

Crow, J., and M. Kimura. 1970. An introduction to population genetics theory. Harper and Row, New York.

Crow, J. F., and N. E. Morton. 1955. Measurement of gene frequency drift in small populations. Evolution 9:202–214.

Cuenco, M. L., T. W. H. Backman, and H. R. Mundy. 1993. The use of supplementation to aid in natural stock restoration. Pages 269–293 *in* J. G. Clous and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum Press, New York.

Cushing, D. H. 1983. Key papers on fish populations. IRL Press Limited, Washington, DC.

Darwin, C. 1859. On the origin of species by natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 6(2):115–143.

Dizon, A. E., C. Lockyer, W. F. Perrin, D. P. Demaster, and J. Sisson. 1991. Rethinking the stock concept: a phylogeographic approach. Conservation Biology 5:24–36.

Dobzhansky, T. 1950. Mendelian populations and their evolution. American Naturalist 84:401–418.

Dobzhansky, T. 1970. Genetics of the evolutionary process. Columbia University Press, New York.

Doyle, R. W., C. Herbinger, C. T. Taggart, and S. Lochmann. 1995. Use of DNA microsatellite polymorphism to analyze genetic correlations between hatchery and natural fitness. Pages 205–211 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15, Bethesda, Maryland.

Emlen, J. M. 1984. Population biology. The coevolution of population dynamics and behavior. MacMillan Publishing Company.

Falconer, D. S. 1989. Introduction to quantitative genetics, third edition. Longman-Harlow, United Kingdom.

Flagg, T. A., F. W. Waknitz, D. J. Maynard, G. B. Milner, and C. V. W. Mahnken. 1995. The effect of hatcheries on native coho salmon populations in the lower Columbia River. Pages 366–375 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium 15, Bethesda, Maryland.

Fleming, I. A., and M. R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecological Applications 3:230–245.

Flexner, S.B., editor. 1993. Random House Unabridged Dictionary, second edition. Random House, Inc., New York.

Fox, W. W. 1991. Policy on applying the definition of species under the Endangered Species Act to Pacific salmon. Federal Register 56 (224):58612–58618.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 *in* M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Geiger, H. J., and A. J. Gharrett. 1998. Salmon stocks at risk: what's the stock, and what's the risk? Alaska Fishery Research Bulletin 4(2):178-180.

Gharrett, A. J., and S. M. Shirley. 1985. A genetic examination of spawning methodology in a salmon hatchery. Aquaculture 47:245–256.

Gharrett, A. J., and W. W. Smoker. 1993a. A perspective on the adaptive importance of genetic infrastructure in salmon populations to ocean ranching in Alaska. Fisheries Research 18:45–58.

Gharrett, A. J., and W. W. Smoker. 1993b. Genetic components in life history traits contribute to population structure. Pages 197–202 *in* J. G. Cloud and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum Press, New York.

Gilmour, J. S. L., and J. W. Gregor. 1939. Demes: a suggested new terminology. Nature 144:333–334.

Gilmour, J. S. L., and J. Heslop-Harrison. 1954. The deme terminology and the units of micro-evolutionary change. Genetics 27:147–161.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Ginsburg, I. 1938. Arithmetical definition of the specie, subspecies, and race concept, with a proposal for a modified nomenclature. Zoologica 23:253-286.

Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. Risk Analysis 2:171–181.

Goodman, D. 1987. The demography of chance extinction. Pages 11–34 *in* M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge.

Grant, V. 1963. The origin of adaptations. Columbia University Press, New York.

Hanski, I., and M. E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Pages 3–16 *in* M. E. Gilpin and I. Hanski, editors. Metapopulation dynamics. Academic Press, New York.

Harrison, J. 1994. Sharing the watershed: Grande Ronde plan protects endangered salmon and the economy of northeast Oregon. Northwest Energy News:15–17.

Helle, J. H. 1981. Significance of the stock concept in artificial propagation of salmonids in Alaska. Canadian Journal of Fisheries and Aquatic Sciences 38:1665–1671.

Higgins, P., S. Dobush, and D. Fuller. 1992. Factors in northern California threatening stocks with extinction. American Fisheries Society, Humbolt Chapter, Arcata, California.

Hilborn, R. 1985. Apparent stock-recruitment relationships in mixed stock fisheries. Canadian Journal of Fisheries and Aquatic Sciences 42:718–723.

Hilborn, R., C. S. Holling, and C. J. Walters. 1980. Managing the unknown: approaches to ecological policy design. American Institute of Biological Sciences.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systems 4:1–23.

Holling, C. S., editor. 1978. Adaptive environmental assessment and management. John Wiley and Sons, New York.

Holling, C. S. 1989. Integrating science for sustainable development. Journal of Business Administration 19 (1 & 2):73–83.

Hyman, J. B., K. Wernstedt, and C. Paulsen. 1993. Dollars and sense under the Endangered Species Act: incorporating diverse viewpoints in recovery planning for Pacific Northwest salmon. Resources for the Future, Washington, DC.

Jimenez, J. A., K. A. Hughes, G. Alaks, L. Grahm, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. Science 266(14):271–273.

Kapuscinski, A. R. D. 1984. A genetic fitness model for fisheries management. Doctoral dissertation, Oregon State University, Corvallis.

Kapuscinski, A. R., and L. D. Jacobson. 1987. Genetic guidelines for fisheries management. Minnesota Sea Grant, St. Paul.

Kapuscinski, A. R., and L. M. Miller. 1993. Genetic hatchery guidelines for the Yakima/Klickitat fisheries project. Washington Department of Fisheries Contract Report.

Kimura, M., and T. Ohta. 1971. Theoretical aspects of population genetics. Princeton University Press, Princeton.

King, R. C., and W. D. Stansfield. 1990. A dictionary of genetics, 4th edition. Oxford University Press, England.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. Conservation Biology 1(2):143–158.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–124 *in* M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

Lande, R., and S. H. Orzack. 1988. Extinction dynamics of age-structured populations. Proceedings of the National Academy of Sciences 85:7418–7421.

Larkin, P. A. 1972. The stock concept and management of Pacific salmon. Pages 11–15 *in* R. C. Simon and P. A. Larkin, editors. The stock concept in Pacific salmon. H. R. MacMillian Lectures in Fisheries, University of British Columbia, Vancouver.

Lee, K. N. 1989. Columbia River basin — experimenting with sustainability. Environment 31(6):7–11, 30–33.

Lee, K. N. 1993. Compass and gyroscope: integrating science and politics for the environment. Island Press, Washington, DC.

Lee, K. N., and J. Lawrence. 1986. Adaptive management: learning from the Columbia River basin fish and wildlife program. Environmental Law 16:431–460.

Leigh, E. G., Jr. 1981. The average lifetime of a population in a varying environment. Journal of Theoretical Biology 90:213–239.

Levings, C. D. 1993. Requirements for genetic data on adaptations to environment and habitats of salmonids. Pages 49–66 *in* J. G. Cloud and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum, New York.

Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260 (17 & 36).

Ludwig, D., and C. J. Walters. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 38(6):711–720.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Mayr, E. 1940. Speciation phenomena in birds. American Naturalist 74:249–278.

Mayr, E. 1954. Notes on nomenclature and classification. Systematic Zoology 3:86–89.

Mayr, E. 1963. Animal species and evolution. The Belknap Press, Cambridge, Massachusetts.

Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

Moyle, P. B., and R. M. Yoshiyama. 1994. Protection of aquatic biodiversity in California: a five-tiered approach. Fisheries 19(2):6–18.

Mundy, P. R., and J. K. Fryer. 1995. Abundance based criteria for recognition of damaged salmon populations. Pages 202–212 *in* Salmon management in the 21st Century: recovering stocks in decline. Proceedings of the 1992 Northwest Pacific chinook and coho workshop. American Fisheries Society, Idaho Chapter, Boise.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4–21.

Nei, M. 1972. Genetic distance between populations. American Naturalist 106:283–292.

Nei, M. 1987. Genetics distance and molecular phylogeny. Pages 193–223 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. Washington Sea Grant, University of Washington Press, Seattle.

Nelson, K., and M. Soulé. 1987. Genetic conservation of exploited fishes. Pages 345–368 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Nielsen, J. L. 1993. Evolution and the aquatic ecosystem: defining significant units in population conservation. American Fisheries Society, Conference Proposal.

NMFS (National Marine Fisheries Service). 1978. Biological basis for listing species of other taxa of salmonids pursuant to the Endangered Species Act of 1973. National Marine Fisheries Service, Workshop Summary, Portland.

Nozawa, K. 1972. Population genetics of Japanese monkeys: I. estimation of effective population size. Primates 13:381–393.

NRC (National Research Council). 1995. Science and the Endangered Species Act. National Academy Press, Washington, DC.

O'Brien, S. J., and J. F. Evermann. 1988. Interactive influence of infectious disease and genetic diversity in natural populations. Trends in Ecological Evolution 3:254–259.

Otte, D., and J. Endler. 1989. Speciation and its consequences. Sinauer, Sunderland, Massachusetts.

Pascual, M. A., and T. P. Quinn. 1994. Geographical patterns of straying of fall chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. Aquaculture and Fishery Management 25 (Supplement 2):17–30.

Paulik, G.J., A.S. Hourston, and P.A. Larkin. 1967. Exploitation of multiple stocks by a common fishery. Journal of the Fisheries Research Board of Canada 24:2527–2537.

Policansky, D. 1993. Fishing as a cause of evolution in fishes. Pages 2–18 *in* T. K. Stokes, J. M. McGlade, and R. Law, editors. The exploitation of evolving resources. Lecture Notes in Biomathematics 99, Springer-Verlag, Berlin.

Quinn, T. P. 1990. Current controversies in the study of salmon homing. Ethology, Ecology & Evolution 2:49–63.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29–44.

Quinn, T. P., R. S. Nemeth, and D. O. McIsaac. 1991. Homing and straying patterns of fall chinook salmon in the lower Columbia River. Transactions of the American Fisheries Society 120:150–156.

Ray, J. 1686. Historia plantarum (volume 1). London.

Reaka-Kudla, M. L., D. E. Wilson, and E. O. Wilson. 1997. Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, DC.

Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature 346:357–359.

Rich, W. H. 1939. Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. American Association of the Advancement of Scientific Publishing 8:45–50.

Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. Theoretical Population Biology 3:406–433.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Ricker, W. E. 1972. Heredity and environmental factors affecting certain salmonid populations. Pages 19–160 *in* R. C. Simon and P. A. Larkin, editors. The stock concept in Pacific salmon. H. R. MacMillian Lectures in Fisheries, University of British Columbia, Vancouver.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin 191, Ottawa, Quebec.

Riddell, B. E., and W. C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 38:308–320.

Rieger, R., A. Michaelis, and M. M. Green. 1991. Glossary of genetics, fifth edition. Springer-Verlag, New York.

Rohlf, D. J. 1991. Six biological reasons why the Endangered Species Act doesn't work — and what to do about it. Conservation Biology 5:273–282.

Rohlf, D. J. 1994. There's something fishy going on here: a critique of the National Marine Fisheries Service's definition of species under the Endangered Species Act. Pages 650–651 *in* Environmental Law IV.F. Northwestern School of Law, Lewis and Clark College, Portland.

Ryder, O. A. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecological Evolution 1:9–10.

Ryman, R., R. Bassus, C. Reuterwall, and M. H. Smith. 1981. Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. *Oikos* 36:257–266.

Schaefer, M. L. 1981. Minimum population sizes for species conservation. BioScience 31(2):131–134.

Schaefer, M. L. 1990. Population viability analysis. Conservation Biology 4:39–40.

Scudder, G. G. E. 1989. The adaptive significance of marginal populations: a general perspective. Pages 180–185 *in* C. D. Levings, L. B. Holtby, and M. A. Henderson, editors. Proceedings of the national workshop on effects of habitat alteration on salmonid stocks. Canadian Special Publication of Fisheries and Aquatic Sciences 105.

Simon, R. C., J. D. McIntyre, and A. R. Hemmingsen. 1986. Family size and effective population size in a hatchery stock of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43:2434–2442.

Smith, A. D. M., and C. J. Walters. 1981. Adaptive management of stock recruitment systems. Canadian Journal of Fisheries and Aquatic Sciences 38:690–703.

Smith, C. L. 1994. Connecting cultural and biological diversity in restoring Northwest salmon. Fisheries 19(2):20–26.

Smith, H. D., L. Margolis, and C. C. Woods, editors. 1987. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96.

Smoker, W. W., A. J. Gharrett, and M. S. Stekoll. *In press*. Genetic variation in timing of anadromous migration within a spawning season in a population of pink salmon. *In* B. E. Riddell, editor. Proceedings of the international symposium on biological interactions of enhanced and wild salmonids. Canadian Special Publication of Fisheries and Aquatic Sciences, Nanaimo.

Smoker, W. W., A. J. Gharrett, M. S. Stekoll, and J. E. Joyce. 1994. Heretability of size in an anadromous population of pink salmon. Canadian Journal of Fisheries and Aquatic Sciences 51 (Supplement):9–15.

Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151–169 *in* M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Soulé, M. E. 1987. Introduction. Pages 1–10 *in* M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge.

Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. BioScience 39:436–446.

STOCS (Stock Composition International Symposium). 1981. The proceedings of the 1980 stock concept international symposium. Canadian Journal of Fisheries and Aquatic Sciences 38(12):1457–1458.

Tajima, F. 1992. Statistical method for estimating the effective population size in Pacific salmon. Journal of Heredity 83:309–311.

Taylor, E. B. 1990. Phenotypic correlates of life history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. Journal of Animal Ecology 59:455–468.

Taylor, E. G. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207.

Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population size? Conservation Biology 4:144–156.

Thompson, G. G. 1991. Determining minimum viable populations under the Endangered Species Act. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Technical Memorandum NMFS F/NWC-198, Seattle.

Thorpe, J. E. 1989. Developmental variation in salmonid populations. Journal of Fish Biology 35 (Supplement A):295–303.

Thorpe, J. E. 1993. Impacts of fishing on genetic structure of salmonid populations. Pages 67–80 *in* J. G. Cloud and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum, New York.

Tobin, R. J. 1990. The expendable future. U.S. Politics and the protection of biological diversity. Duke University Press, Durham, North Carolina.

Utter, F. M. 1980. Cover document for working reports on the Endangered Species Act. Coastal Zone and Estuarine Studies.

Utter, F. M. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. Canadian Journal of Fisheries and Aquatic Sciences 38:1626–1635.

Utter, F. M., W. J. Ebel, G. B. Milner, and D. J. Teel. 1982. Population structures of fall chinook salmon, *Oncorhynchus tshawytscha*, of the mid-Columbia and Snake Rivers. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Processed Report 82-10, Seattle.

Utter, F. M., J. E. Seeb, and L. W. Seeb. 1993. Complementary uses of ecological and biochemical genetic data in identifying and conserving salmon populations. Fisheries Research 18:59–76.

Utter, F. M., R. S. Waples, and D. J. Teel. 1992. Genetic isolation of previously indistinguishable chinook salmon populations of the Snake and Klamath Rivers: limitations of negative data. Fisheries Bulletin 90:770–777.

Van Alen, B. *In press*. Status and stewardship of salmon stocks in Southeast Alaska. Proceedings of the conference towards sustainable fisheries: balancing conservation and use of salmon and steelhead in the Pacific Northwest. Ann Arbor Press, Ann Arbor, Michigin.

Vance, R. R. 1980. The effect of dispersal on population size in a temporally varying environment. Theoretical Population Biology 18:343–362.

Vincent, R. E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchell). Transactions of the American Fisheries Society 89:35–52.

Volkman, J. M., and W. E. McConnaha. 1993. Through a glass, darkly: Columbia River salmon, the Endangered Species Act, and adaptive management. Environmental Law 23:1249–1272.

Walters, C. J. 1981. Optimum escapements in the face of alternative recruitment hypotheses. Canadian Journal of Fisheries and Aquatic Sciences 38(6):678–689.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan Publishing Company, New York.

Walters, C. J., R. D. Goruk, and D. Radford. 1993. Rivers Inlet sockeye salmon: an experiment in adaptive management. North American Journal of Fisheries Management 13:253–262.

Walters, C. J., and R. Hilborn. 1976. Adaptive control of fishing systems. Journal of Fisheries Research Board of Canada 33:145–159.

Walters, C. J., and C. S. Holling. 1984. Resilience and adaptability in ecological management systems: why do policy models fail? International Series on Applied Systems Analysis 13 (1984).

Waples, R. S. 1990. Conservation genetics of Pacific salmon II. Effective population size and the rate of loss of genetic variability. Journal of Heredity 81:267–276.

Waples, R. S. 1991a. Definition of "species" under the Endangered Species Act: application to Pacific salmon. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Technical Memorandum NMFS F/NWC-194.

Waples, R. S. 1991b. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 48 (Supplement 1):124–133.

Waples, R. S. 1991c. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53(3):11–22.

Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *In* J. L. Nielsen and D. A. Powers, editors. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17, Bethesda, Maryland.

Waples, R. S., D. J. Teel, and P. B. Aebersold. 1991. A genetic monitoring and evaluation program for supplemented populations of salmon and steelhead in the Snake River basin. National Marine Fisheries Service, Northwest Fisheries Science Center, Portland.

Wiley, E. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. Wiley, New York.

William, W. F., Jr. 1991. Policy on applying the definition of species under the Endangered Species Act to Pacific salmon. Federal Register 56:58612–58618.

Withler, R. E., and T. P. T. Evelyn. 1990. Genetic variation in resistance to bacterial kidney disease within and between two strains of coho salmon from British Columbia, Canada. Transactions of the American Fisheries Society 119(6):1003–1009.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Wright, S. 1940. Breeding structure of populations in relation to speciation. American Naturalist 74:232–248.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics 15:323–354.

Wright, S. 1955. Classification of the factors of evolution. Cold Spring Harbor Symposium, Quantitative Biology 20:16–24D.

Wright, S. 1969. Evolution and the genetics of populations, volume 2: the theory of gene frequencies. University of Chicago Press, Chicago.